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Influence of MHC on odour perception of 43 chemicals and body odour

Research Article

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Abstract: The Major Histocompatibility Complex (MHC) is a large gene family that is found in most vertebrates and has an important influence on body odour preference and mate selection in animals. In this research we found, that human leukocyte antigen (HLA) phenotype is strongly connected with the strength and pleasantness of perceived odour of selected chemical compounds found in sweat. Among different chemical classes of compounds tested, the esters of fatty acids such as methyl undecanoate, methyl decanoate, methyl nonanoate, methyl octanoate and methyl hexanoate show strongest connection to HLA. On the other hand, our experiment did not confirm the connection of MHC to the perceived strength and pleasantness of body odour.

Keywords: *Major histocompatibility complex (MHC) • Human leukocyte antigens (HLA) • Odour perception • Sweat • Methyl hexanoate • Musk*

1. Introduction

The major histocompatibility complex (MHC), known in humans as HLA (human leukocyte antigens), consists of immunoglobulin-like cell surface proteins, responsible for presentation of antigenic peptides to T cells in order to control self/nonself immune recognition. Highly polymorphic HLA genes are located on a short arm of chromosome 6. MHC has a significant influence on mating preference in many animals (reviewed in [1]). This system is important for mate selection in mice [2,3], salmon [4] and birds [5,6]. In mice the odour of urine plays a crucial role in this process [7]. MHC-mediated mate choice has been shown to increase parasite resistance in salmon [8].

In humans, the connection between the MHC and mate choice or body odour preference is still controversial. While the MHC has been shown to be involved in body odour preference in a Swiss population [9,10], an isolated Hutterites community of Austrian descendants in USA [11], a Brazilian [12] and a British population [13]; in an ethnically mixed American population, only men showed a preference for T-shirts with the scent of MHC dissimilarity [14]. Furthermore, although a connection between MHC and mate choice was found in Hutterites [15], it was not identified in a Japanese population [16]. Studies on the linkage between MHC and human mate choice were recently reviewed by Havlicek and Roberts [1].

Although the mechanism of MHC related preferences is not clear, studies on rodents together with available human data suggests that body odour is one of the most important pathways. While it has been shown that MHC is correlated to the perfume preference [17], it is not yet known, which chemical components of the body odour are responsible for this MHC dependant phenomenon. In this study, volunteers with different HLA phenotypes were asked to assess the intensity and pleasantness

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of 43 single chemical compounds that have been reported to be present in human odour [18,19] including fatty acid esters, ketones, aldehydes, alcohols and sulphur compounds. Sulphur compounds are known to be MHC-related in mice [7] and their perception is supposed to be genetically dependent also in humans [20]. Our volunteers also evaluated the odour of a set of natural and synthetic musk compounds. Natural musk compounds are well known for their function in mating and reproduction [21-23]. Additionally, a connection of MHC with body odour preference was tested in our experimental group as well.

2. Experimental Procedures

2.1 Participants

All volunteers attended a lecture about the research plan, where specific instructions for body odour collection were presented. After the lecture, basic participant information needed for this study was collected. A total of 32 participants, 16 female and 16 male, aged between 20 to 42 years old took part in this study. Two pairs of siblings were in the group, ten of the volunteers were smokers and six of the females were taking oral contraceptives

2.2 Chemicals

The chemicals used for odour estimation and their codes are listed in Table 1. Musk xylene (M15) was synthesized according to the standard procedure for nitro musks [24]. All other chemicals were commercially available (Fluka, Buchs, Switzerland: S16, S13, S12, S10, S24, S17, S27, S6, S7, S1, S2, S3, S23, S25, M9, M16; Sigma-Aldrich, Steinheim, Germany: S14, S15, S11, S18, S5, S26, S21, S22, S8, S19, S20, M1, M2, M3, M8, M13; Riedel de Haën, Seelze bei Hannover, Germany: S9; Merck, Darmstadt, Germany: S4; PFW Aroma chemicals, MT Barneveld, The Nederlands: M6; International Flavors & Fragrances, New York, USA: M4, M5, M7, M14; Firmenich SA, Geneva, Switzerland: M10, M11; M12).

As substance concentration can influence the perceived pleasantness and intensity of the odour, preliminary tests were undertaken on three assessors to find an optimal concentration and method of assessing odour. Two different concentrations (1% and 0.1%) and two different methods (solution and paper strips) were used. The most suitable combination was chosen for each substance. Samples of chemicals S1 to S27 were prepared as 1% solutions in 96% ethanol (except S17, S19 and S20 which were prepared as 0.1% solutions) in 2 ml brown-glass bottles, and their odour was assessed directly from the bottles. Samples of chemicals M2 to M16 were prepared as 1% solutions in 96% ethanol and sample M1 was prepared as 0.1% solution. Aliquots of 100 µl of sample solutions M1 to M16 were applied on a respective odour strip (Rotilabo® 6 x 135 mm odour strips made of filter carton 240 g/m^2 (Carl Roth, Karlsruhe, Germany). Odour strips were used for odour estimation not earlier than 3 min (to enable ethanol to evaporate) and not later than 20 minutes after they were soaked with test solutions.

2.3 Body odour collection procedure

The method of sampling body odour (e.g. duration of sampling, skin area) is important to the perception of the odour. To be able to compare our results to other studies, we adopted the approach used by in most previous studies [9-11,13,14]. In brief, each participant was given a white, 100% cotton T-shirt (washed with unscented detergent), a bottle of unscented shower gel and a large plastic bag. Participants were instructed to refrain from using perfume, engaging in sexual activity, sharing their bed with anyone, and eating onion, garlic, spicy food, drinking alcohol or chewing gum during the days on which body odour was collected. Participants were asked to wear T-shirt for two consecutive nights, after taking a shower with the unscented shower gel. During the day, they left their T-shirt lying on their bed. Following the second night, the T-shirt was placed in a plastic bag, labelled with their unique code and brought it to the body odour rating session.

2.4 Body odour rating session

The rating procedure was conducted in a large, well-ventilated lecture room. The T-shirts contained in numbered plastic bags, were placed at least one metre apart. Each participant stood next to a randomly picked bag containing a single T-shirt, opened the bag and smelled the T-shirt for 30 seconds. The participants were then instructed to close the bag and rated the smell. After a 30 second interval, the participants moved to the next bag containing a T-shirt, until all T-shirts were scored.

Participants rated the odour for its intensity (0=cannot smell anything to 10=very intense) and pleasantness (1=very unpleasant to 10=very pleasant). In addition, participants also wrote down if the odour reminded them of tobacco, perfume, *etc*. In this way, it was checked if the T-shirt owner strictly followed the body odour collection protocol.

2.5 Chemical compounds odour rating session

The participants rated the odour of 43 chemical compounds in two separate sessions at least one week

	Locus	HLA-A				HLA-B				HLA-DR					
	Antigen	3	2	24	68	35	51	7	15	11	1	7	15	3	16
	N_1	8	17	6	5	8	5	7	6	10	8	7	6	5	5
	N_2	23	14	25	26	23	26	24	25	21	23	24	25	26	26
S23	methyl tetradecanoate														▲
S1	methyl dodecanoate														
S2	methyl undecanoate				↓				↓					↓	
S3	methyl decanoate				↓									↓	
S26	methyl nonanoate													↓	↓
S7	methyl octanoate	▼					↑		↑				↑		
S27	methyl hexanoate				↓		↑					▼			▲
S21	dimethyl adipate														
S22	dimethyl malonate														
S10	tetradecanal														
S11	undecanal						↑								
S12	decanal														
S13	nonanal														
S14	octanal														
S15	heptanal														
S16	hexanal														
S18	trans-2-nonenal														
S9	benzaldehyde														
S5	furfural														
S8	metyl furoate														
S6	ethyl hexanoic acid														
S4	benzyl alcohol								↓						▼
S17	p-cresol														
S19	bis(methyltio)metane														
S20	3-(methyltio)-1-hexanol											↓			
S24	6-methyl-5-hepten-2-one			▲											
S25	α-pinene			▲											
M1	α-androstenol														↑
M3	ethylene brassylate		▲										▼		
M7	ambrettolide														
M8	ω-pentadecanolide														▼
M10	muscone											↓			▼
M9	cyclopentadecanone														
M11	civettone														
M12	exaltenone														
M4	Galaxolide® 50 IPM														
M5	Celestolide														
M6	Tonalid®				↓										
M14	Cashmeran®				↓							↓			▲↓
M15	musk xylene														
M16	musk ketone				▼	▼						▼			
M13	ambroxide											▲			
M2	spermine														

Table 1. Influence of HLA specificities on estimation of odour. Individual HLA antigens are correlated with estimation of higher (▲) or lower (▼) intensity or higher (↑) or lower (↓) pleasantness of odour of individual substance tested ($P<0.01$). N_1 is the number of volunteers possessing respective antigen and N_2 is the number of volunteers without respective antigen. Among different chemical classes of compounds tested, a pattern shows that the esters of fatty acids have strongest connection to HLA.

apart (standards S1 to S27 refer to session one and standards M1 to M16 refer to session two). The rating procedure was conducted in a large, well ventilated lecture room. Samples of chemical compounds, marked with appropriate codes, were at least one meter apart. Each participant started a session at a randomly

selected sample. Participants smelled each sample for 30 seconds and then during the 30 second break, they moved to the next one, until each participant rated all samples.

Participants rated the odour for its intensity (0=cannot smell anything to 10=very intense) and pleasantness (1=very unpleasant to 10=very pleasant). They also wrote down if odour associated them on anything.

2.6 Low resolution HLA typing

Genomic DNA was extracted from peripheral blood samples of participants using the GenoM-6 automated system (Qiagen, Austria). HLA phenotypes were determined with the LABType SSO (One Lambda, Inc., Canoga Park, CA, USA) instrumentation according to the manufacturer's instructions. Briefly, a locus-specific (HLA-A, -B and –DRB1) biotinylated PCR amplicon is produced, denatured, and re-hybridized to a HLA-type-sequence-specific complementary oligonucleotide probes, conjugated to fluorescently coded beads. The bound biotinylated PCR product is than detected in a flow analyzer by using R-phycoerythrin-conjugated streptavidin and the phenotype (HLA-A, -B, -DRB1) of each individual determined by dedicated software. The HLA phenotype similarity between each pair of individuals was calculated as a number of shared HLA antigens on all 3 HLA loci. The lowest similarity was marked 0 (no identical antigens in two individuals), and the highest similarity 6 (all antigens in two individuals are identical at the low resolution HLA typing).

2.7 Statistical analyses

The influence of HLA on perception of odour of chemical compounds was tested using Student's t-test (with or without assumption of equal variances as required by Levene's Test for Equality of Variances), to compare the odour intensity of respective substance (and separately, in the same way, for its pleasantness) as estimated by individuals with or without the respective HLA antigen (Table 1). For the 9 parameters (intensity estimates for 6 substances and pleasantness estimates for 3 substances) where the normality of distribution was not demonstrated by Kolmogorov-Smirnov Test, an additional nonparametric Mann-Whitney Test was performed, but no differences in results were found. The influence of respective antigen was analysed if it was present in at least 5 volunteers.

Statistical analyses of body odour estimation data were performed by ANOVA on two data sets. The first one (ITT data set) was composed of all 1024 body odour estimations (32 assessors rating 32 T-shirts). The second one (PP data set) did not contain the data acquired from 4 T-shirts that were evaluated as being contaminated by tertiary odours (perfume, cigarette smoke, food smells) and hence consisted of 896 body odour estimations (32 assessors rating 28 T-shirts). Additional statistical test was performed excluding the females using oral contraception.

3. Results and Discussion

We found, that MHC is strongly connected with the strength and pleasantness of perceived odour of the compounds that are found in human sweat. Significant correlations between HLA antigens and the estimation of odour intensity or pleasantness are presented in Table 1. Odour intensity of methyl hexanoate was estimated to be significantly stronger by individuals with HLA-DR16, than by those without this antigen ($P<0.001$). On the other hand, the odour intensity of methyl octanoate was estimated as significantly weaker by individuals carrying HLA-A3, compared to those without it ($P<0.001$). Similarly, the intensity of musk

assesor	male				male				female				female			
assesed	male				female				male				female			
HLA difference	intensity		pleasantness		intensity		pleasantness		intensity		pleasantness		intensity		pleasantness	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
0	4.77	2.52	3.96	2.21	4.13	2.38	4.82	2.33	6.38	2.69	5.13	3.07	6.32	2.97	5.47	2.99
1	4.80	2.54	4.05	2.13	4.42	2.58	4.85	2.44	5.91	2.85	4.41	2.72	5.97	2.13	5.56	2.63
2	4.68	2.36	4.19	2.31	4.73	2.66	5.47	2.23	5.86	2.82	4.06	2.75	5.80	2.67	5.27	2.71
3	3.83	2.29	4.55	1.97	3.94	2.71	4.73	1.83	5.22	2.02	4.33	1.81	5.67	1.86	7.33	1.03
4	4.75	2.22	3.00	1.41	4.00	2.65	2.50	0.71	8.67	1.53	6.33	4.04	8.00	0.00	3.00	2.83
self	3.07	1.98	4.86	1.75									4.21	2.55	5.75	2.80
Total	4.61	2.47	4.10	2.15	4.35	2.54	4.95	2.32	6.02	2.74	4.57	2.81	5.91	2.55	5.51	2.72
ANOVA	0.159		0.599		0.70		0.29		0.22		0.24		0.106		0.434	
N	240		228		223		200		210		199		196		192	

Table 2. Average intensity and pleasantness of body odour scores (±SD) assessed by volunteers after smelling T-shirts of other study participants, as a function of interindividual HLA (dis)similarity in respective subgroups. No significant difference was found in any subgroup.

ketone was estimated significantly weaker by individuals possessing HLA-A68 (P<0.001). In relation to odour pleasantness, the most significant connection was found between methyl hexanoate and the expression of HLA-B51 (P<0.001). Fatty acids methyl esters are involved in three out of four above mentioned highly significant connections. To minimise type I errors, the significance criteria (α) was adjusted from 0.05 to 0.01. Due to multiple t-tests (43 chemicals x 14 genotypes x 2 intensity/pleasantness ratings=1204 comparisons) 12 of the 37 significant correlations between HLA and odour preference noted in Table 1 may occur by chance. As avoidance of type II errors (to reject true hypothesis) at the expense of an elevated type I error rate (to accept false hypothesis) is recommended in exploratory studies [25], we did not lower α below 0.01 to avoid excessive type II error. Among different chemical classes of compounds tested, fatty acids esters including methyl undecanoate, methyl decanoate, methyl nonanoate, methyl octanoate and methyl hexanoate showed the strongest connection to HLA phenotype. This class of compounds is involved in 12 out of 21 connections between HLA and odour pleasantness (marked with arrows in the Table 1). This clearly demonstrates that fatty acids esters are the most probable candidates to explain connection between HLA and body odour preference.

When estimations of body odour on the T-shirts were analysed, each individual rated their own T-shirt differently when compared to the corresponding estimations given for the same T-shirt by other participants. The individuals perceived their own odour as less intense and estimated it on average 1.4 point lower (paired-samples t-test: P=0.0018). On the other hand, the average estimation of pleasantness of own odour was only 0.02 points higher than the estimation given by others (P=0.11). This effect is most probably the consequence of adaptation to own odour and is not connected to HLA dependant self-identity. Therefore, we decided to exclude all self-estimations from further analyses.

In the group of volunteers, 257 pairs did not share any common HLA specificity, 328 pairs shared 1 antigen, 190 pairs shared 2 antigens, 54 pairs shared 3 antigens and 12 pairs shared 4 HLA antigens (low resolution typing). The correlation between the number of HLA alleles shared by estimating and estimated volunteer (so called “HLA similarity”) and the odour estimation was analysed. In addition to standard statistical analyses on total ITT and PP sets, separate tests were undertaken for male volunteers estimating female odour and female volunteers estimating male odour (Table 2). Furthermore, an additional test excluding female volunteers who used oral contraceptives was also

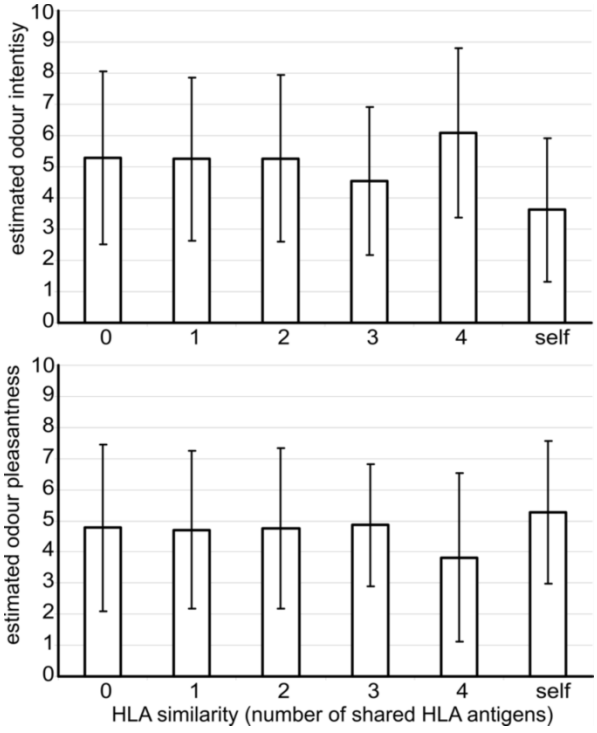

Figure 1. Average intensity and pleasantness of body odour scores (±SD) assessed by volunteers after smelling T-shirts of other study participants, as a function of interindividual HLA (dis)similarity. Column “HLA similarity 0” represents the average score of 257 odour estimations where assessed volunteer and assessing volunteer did not share any common HLA specificity, column 1 is the average of 328 pairs sharing 1 antigen, column 2 is the average of 190 pairs sharing 2 antigens, column 3 is the average of 54 pairs sharing 3 antigens and column 4 is the average of 12 pairs sharing 4 HLA antigens. Column marked with "self" represents average estimations of volunteers smelling their own T-shirts. In our experimental group we did not find any statistically significant correlation between HLA similarity/diversity and body odour preference.

performed. Interestingly, this mixed model technique did not significantly change the relationship between MHC and body odour preferences.

Surprisingly, no statistically significant relationship between MHC and the perceived intensity or pleasantness of body odour was observed with any of the data sets tested (Figure 1). The reason why such connection was found in Swiss [9-10], in isolated community of Austrian descents in USA [11] and Brazilian [12] population, but not in Slovenian population, can be in higher heterogeneousness of Slovenian population which is situated at the junction of Slavic (Croat and Slovenian), German (Austrian), Romanic (Italian) and Finno-Ugric (Hungarian) nations.

The diversity of HLA-A, -B and –C in Slovenian population was first studied in a population sample of 100 randomly chosen Slovenians with the first generation of their forefathers having had declared

themselves as Slovenians and representing all parts of our country [26]. The assessment of DRB1, DQB1, DQA1, DPB1 and DPA1 loci as well as DQB1 and DQA1 promoter regions was performed by Vidan-Jeras *et al.* [27,28]. In a study of global allele distributions, the DPB1*0401 was observed at a very high frequency in Slovenian population while the frequency in surrounding European populations was low [27,29]. Different allele frequencies were also observed in a comparative study of HLA B44 allelic subtypes and their A-B-DR haplotypes in a Slovenian, Dutch and Swiss population. In contrast to the Dutch and Swiss population, where the B*4402 allele is predominantly linked to HLA-A2 allele, the prevailing linkage in Slovenians is with HLA-A24 and A28 [30]. The B*4403 allele was linked to DR7 allele in 82% of all B*4403 haplotypes in Swiss population and less so in Dutch (72%) and Slovenian (59%) populations [30]. In the Swiss population more than a half of B44-DR7 haplotypes were of one single subtype (A23-B*4403-DR7), while this was significantly lower in Dutch (14%) and even less in Slovenian population (6%) [30]. All these results clearly show a certain degree of MHC heterogeneity in Slovenian population that is specific as compared to neighbouring nations and others in the world.

In this study, the number of odour assessments was 1024 (32 rates rating 32 T-shirts) while the numerous in other above mentioned studies was 726, 294 and 1676, respectively, and the study design was similar. The most important difference in design of this study was the number of odour assessments volunteers were asked to undertake. In comparison with other experiments whereby volunteers assessed 6 odours [9-11], 32 odour assessments were made in this study. While it is possible that a sensory overload may affect the results obtained in this study, a previous study by Santos *et al.* (2005) [12] assessed 58 odours although divided in two separate sessions.

A larger sample size will be needed to exclude any connection between HLA genotype and perception of body odour in Slovenian population, but the connection between HLA genotype and perception of the odour of fatty acid methyl esters was clearly shown in this study.

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